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Three new species of *Hydnophlebia* (Polyporales, Basidiomycota) from the Macaronesian Islands

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Abstract

The genus *Hydnophlebia* includes two species of wood-inhabiting fungi, *Hydnophlebia chrysorhizon* and *Hydnophlebia omnivora*. Both are characterized by cream to reddish-orange, resupinate basidiome, with hydnoid hymenophore, margin with strands, a monomitic hyphal system, tubular to ventricose cystidia and elliptical spores. In this paper, a taxonomic study of *Hydnophlebia*, using morphology and molecular analyses of large subunit nuclear ribosomal DNA (LSU) and the internal transcribed spacer nrDNA operon (ITS), is reported. Three new species, *Hydnophlebia canariensis*, *H. gorgonea* and *H. meloi*, from the Macaronesia bioregion (Canary Islands and Cape Verde Archipelago), are described.

Keywords

Agaricomycetes, corticioid fungi, phylogeny, taxonomy, Canary Islands, Cape Verde Archipelago

Introduction

Hydnophlebia was erected by Parmasto (1967) to accommodate *Hydnum chrysorhizon* Torr. A few years later, the type species was transferred to *Phanerochaete* P. Karst. (Budington and Gilbertson 1973), and *Hydnophlebia* was neglected for a long time. Ryvarden et al. (2005) reintroduced it with a brief description taken from the original Latin diagnosis: basidioma resupinate, membranous, reddish-orange, hymenophore hydnoid with aculei, margin with rhizomorphs, hyphal system monomitic, tubular to

ventricose usually few cystidia, and spores ellipsoid, smooth, and thin-walled. According to Hjortstam and Ryvarden (2009), two species should be included in this genus of wood-inhabiting corticoid fungi: *Hydnophlebia chrysorhizon* (Torr.) Parmasto and *Hydnophlebia omnivora* (Shear) Hjortstam & Ryvarden.

Parmasto (1968) included *Hydnophlebia* in tribe Byssomerulieae (Corticiaceae) together with other genera, such as *Byssomerulius* Parmasto, *Chaetoderma* Parmasto, *Crustoderma* Parmasto, and *Phanerochaete*, while Larsson (2007), in his phylogenetic classification for corticioid fungi, included it in Meruliaceae, Polyporales. More recently, Floudas and Hibbett (2015) presented a four gene phylogenetic analysis of phanerochaetoid taxa and confirmed *Phanerochaete* as polyphyletic and *Hydnophlebia* as a genus of its own.

During our survey of corticioid fungi from Macaronesia (Canary Islands and Cape Verde Archipelago), nine hydnoid specimens were initially identified as belonging to the genus *Phanerochaete*. BLAST search of the large subunit of the nrDNA (LSU) sequences showed high similarity with a sequence published in Wu et al. (2010) and identified as *Phanerochaete chrysorhizon* (Torr.) Budington & Gilb. (AF139967). In the analysis by Wu et al. (2010) this sequence was recovered within a clade (clade V) containing i.a. *Phlebia* sensu stricto and a number of taxa with typically odontoid or hydnoid hymenophore, quite far from the *Phanerochaete* core group. BLAST search of the internal transcribed spacers of the nuclear ribosomal gene (ITS) sequences, which gave high similarity to sequences labelled as *Phanerochaete chrysorhizon* (AY219359) and *Phanerochaete omnivora* (Shear) Burdsall & Nakasone (AY219360) published in de Koker et al. (2003). Like later Wu et al. (2010) also de Koker et al. (2003) found that these taxa were not related to the *Phanerochaete* core group.

The aim of this study was to characterize and classify our specimens from Macaronesia, using morphological data and molecular analyses of LSU and ITS regions.

Materials and methods

Sampling, morphological studies and line drawings

Specimens were collected in the Canary Islands and Cape Verde Archipelago (Table 1), and are deposited in the mycological collection (MA-Fungi) of the Real Jardín Botánico herbarium in Madrid, Spain; the initials MD correspond to M. Dueñas, and Tell. to M.T. Telleria. The type specimens of *Hydnum chrysorhizon* (NY!) and *Hydnum omnivorum* Shear (BPI!) were included in the morphological analyses. Colours of dried basidiomata are given according to ISCC-NBS Centroid Color Charts (Kelly and Judd 1976). Dried specimens were also used for light microscope studies and drawings. Measurements and drawings were made from microscopic sections mounted in 3% aqueous KOH and/or Congo Red solution and examined at magnifications up to 1250× using an Olympus BX51 microscope. The length and width of 30 spores and 10 basidia were measured from each sample. Line drawings were made with a Leica DM2500 microscope with the aid of a drawing tube.

DNA isolation and sequencing

Genomic DNA was extracted from eight collections (Table 1) using DNeasy® Plant Mini Kit (QIAGEN, Valencia, CA), following the manufacturer's instructions. Basidiomes were disrupted using Tissue-Lyser II (QIAGEN, Germany) and glass beads. Lysis buffer incubation was overnight at 55 °C.

Total DNA was used for PCR amplification of the D1–D2 region of the large subunit (LSU) and the internal transcribed spacer region (ITS) of the nuclear ribosomal gene. The primers LR0R (Rehner and Samuels 1994) and LR7 (Vilgalys and Hester 1990) were used to amplify the region of the LSU nrDNA; the primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990) were used to obtain amplifications of both ITS regions, including the 5.8S of the ribosomal RNA gene cluster and flanking parts of the small subunit (SSU) and large subunit (LSU) nuclear ribosomal genes. Individual reactions to a final volume of 25 µL were carried out using illustra™ PuReTaq™ Ready-To-Go™ PCR Beads (GE Healthcare, Buckingham) with a 10 pmol/µL primer concentration, following the thermal cycling conditions used in Martín and Winka (2000).

Negative controls lacking fungal DNA were run for each experiment to check for contamination. The reactions were run with the following parameters for the LSU nrDNA: initial denaturation at 94 °C for 5 min, then 36 cycles of denaturation at 94 °C for 30 s, annealing at 52 °C for 30 s, and extension at 72 °C for 1.5 min, with a final extension at 72 °C for 10 min, and 4 °C soak; for the ITS nrDNA: initial denaturation at 95 °C for 5 min, then 5 cycles of denaturation at 95 °C for 30 s, annealing at 54 °C for 30 s, and extension at 72 °C for 1 min, followed by 33 cycles of denaturation at 72 °C for 1 min, annealing at 48 °C for 30 s, and extension at 72 °C, with a final extension at 72 °C for 10 min and 4 °C soak.

PCR products were checked on 2% agarose D1 low EEO (CONDA, Pronadisa™) gels and subsequently purified using the QIAquick Gel PCR Purification (QIAGEN) kit according to the manufacturer's instructions. The purified PCR products were sequenced using the same amplification primers at Macrogen Korea (Seoul, Korea).

Sequencher v. 4.2 (Gene Codes Corporation, Ann Arbor, MI) was used to edit the resulting electropherograms and to assemble contiguous sequences (Table 1 in bold). BLAST searches (Altschul et al. 1997), using the MEGABLAST option were done to compare the sequences obtained against the sequences in the EMBL/GenBank/DDBJ databases (Cochrane et al. 2011, 2016).

Sequence alignment and phylogenetic analyses

The LSU and ITS sequences obtained were aligned separately using Se-Al v. 2.0a11 Carbon (Rambaut 2002) for multiple sequences.

To infer phylogenetic relationships of Macaronesian specimens within Meruliaceae, the LSU sequences were compared with homologous sequences retrieved from the

Table 1. Specimens of *Hydnophlebia* species described as new, and EMBL/GenBank/DDBJ and UNITE accessions included in the LSU and ITS nrDNA analyses. The asterisk (*) after the taxon names denotes type species of the genus. The specimens with uncertain generic placement are listed at the end of the table; in Fig. 1 and 2, the uncertainty is indicated by brackets around the name. Isolates and/or voucher specimens are indicated as they appear in GenBank and UNITE accessions.

Names after our LSU or ITS analyses	Names included in EMBL/GenBank/DDBJ and UNITE	Isolate/Voucher	GenBank/UNITE accessions	
			LSU	ITS
*Abortiporus biennis**	*Abortiporus biennis*	KEW210	AF287842	–
*Cabaladontia queletii**	*Phlebia queletii*	FCUG 722, culture	AF141626	–
*Ceriporia viridans**	*Ceriporia viridans*	FO24398	AJ406518	
*Ceriporiopsis gilvescens**	*Ceriporiopsis gilvescens*	O/Haussknecht98	DQ144618	–
*Climacodon septentrionalis**	*Climacodon septentrionalis*	HHB-13438-sp	AF518610	–
*Crustodontia chrysocreas**	*Phlebia chrysocreas*	FPL-6080	AY293199	–
*Crustodontia chrysocreas**	*Phlebia chrysocreas*	KHL10216 (GB)	AY586695	–
*Cymatoderma elegans**	*Cymatoderma elegans*	Halling9064 (NY)	JN649341	–
Hydnophlebia canariensis	*Hydnophlebia canariensis*	17035Tell., MA-Fungi 86622, Holotype	**KF528103**	**KF483012**
Hydnophlebia canariensis	*Hydnophlebia canariensis*	17038Tell., MA-Fungi 86623	**KF528104**	**KF483013**
Hydnophlebia canariensis	*Hydnophlebia canariensis*	17674Tell., MA-Fungi 86619	**KF528100**	**KF483009**
*Hydnophlebia chrysorhizon**	*Phanerochaete chrysorhizon*	FP-102002-sp (CFMR)	–	AY219359
*Hydnophlebia chrysorhizon**	*Phanerochaete chrysorhizon*	T-484, RGT 871020/12	AF139967	–
*Hydnophlebia chrysorhizon**	*Hydnophlebia chrysorhizon*	T 484	–	KP135335
*Hydnophlebia chrysorhizon**	*Hydnophlebia chrysorhizon*	FP-134985	–	KP135336
*Hydnophlebia chrysorhizon**	*Hydnophlebia chrysorhizon*	HHB-18767	–	KP135337
*Hydnophlebia chrysorhizon**	*Hydnophlebia chrysorhizon*	FD-282	–	KP135338
Hydnophlebia gorgonea	*Hydnophlebia gorgonea*	13327MD, MA-Fungi 86642	**KF528122**	**KF483031**
Hydnophlebia gorgonea	*Hydnophlebia gorgonea*	19110Tell., MA-Fungi 86658	**KF528139**	**KF483048**
Hydnophlebia gorgonea	*Hydnophlebia gorgonea*	19111Tell., MA-Fungi 86659, Holotype	**KF528140**	**KF483049**
Hydnophlebia gorgonea	*Hydnophlebia gorgonea*	19133Tell., MA-Fungi 86664	**KF528145**	**KF483054**
Hydnophlebia meloi	*Hydnophlebia meloi*	19071Tell., MA-Fungi 86654, Holotype	**KF528135**	**KF483044**
Hydnophlebia omnivora	*Phanerochaete omnivora*	HHB-5969-sp	–	AY219360
Hydnophlebia omnivora	*Hydnophlebia omnivora* 2[a]	ME-497	–	KP135332
Hydnophlebia omnivora	*Hydnophlebia omnivora* 2[a]	HHB-6228-sp	–	KP135333
Hydnophlebia sp. 1	*Hydnophlebia omnivora* 1[a]	KKN-112-sp	–	KP135334
Hydnophlebia sp. 2	*Phlebia* sp.	TU108437	–	UDB016816
*Junghuhnia crustacea**	*Junghuhnia crustacea*	X1127, O. Miettinen 13852,1 (H)	JN710554	–
*Junghuhnia crustacea**	*Junghuhnia crustacea*	X262, O. Miettinen 2954,1 (H)	JN710553	–
*Lamelloporus americanus**	*Lamelloporus americanus*	X670, T. Laessoe 10119 (O, H)	JN710567	–
*Lilaceophlebia livida**	*Phlebia livida*	FCUG 2189, culture	AF141624	–
*Merulius tremellosus**	*Phlebia tremellosa*	FPL-4294	AY293200	–
*Merulius tremellosus**	*Phlebia tremellosa*	FCUG 1813, culture	AF141632	–
*Merulius tremellosus**	*Phlebia tremellosa*	F15198 (UBC)	DQ384584[b,c]	DQ384584[b,c]

Names after our LSU or ITS analyses	Names included in EMBL/ GenBank/DDBJ and UNITE	Isolate/Voucher	GenBank/UNITE accessions	
			LSU	ITS
*Merulius tremellosus**	*Phlebia tremellosa*	CIRM-BRFM 968	–	GU731568
*Mycoacia fuscoatra**	*Mycoacia fuscoatra*	KHL13275 (GB)	JN649352	JN649352
*Mycoacia fuscoatra**	*Phlebia subserialis*	KUC8041, culture	AY858370	
Mycoacia nothofagi	*Mycoacia nothofagi*	KHL13750	GU480000	–
Mycoacia nothofagi	*Phlebia nothofagi*	AH31887	GQ259416	–
Mycoacia nothofagi	*Phlebia nothofagi*	KHL13750	GU226430	–
*Mycorrhaphium adustum**	*Mycorrhaphium adustum*	KHL12255 (GB)	JN710573	–
*Mycoaciella bispora**	*Mycoaciella bispora*	EL13_99	AY586692	–
Phlebia acerina	*Phlebia acerina*	FCUG 568, culture	AF141615	–
*Phlebia radiata**	*Phlebia radiata*	culture?	AB325676	–
*Phlebia radiata**	*Phlebia radiata*	FCUG2423, culture	AF141627	–
*Phlebia radiata**	*Phlebia radiata*	FPL6140	AF287885	–
*Phlebia radiata**	*Phlebia radiata*	GEL5258	AJ406541	–
*Phlebia radiata**	*Phlebia radiata*	KUC8034, culture	AY858369	–
*Phlebia radiata**	*Phlebia radiata*	TM03_491	EU522844	–
*Phlebia radiata**	*Phlebia radiata*	JLL-15608-sp. (CFMR)	–	AY219366
*Phlebia radiata**	*Phlebia radiata*	ATCC 64658, culture	–	EF491867
Phlebia rufa	*Phlebia rufa*	FCUG 2397	AF141628	–
*Scopuloides hydnoides**	*Scopuloides hydnoides*	KHL11916 (GB)	EU118665[c]	EU118665[c]
*Scopuloides hydnoides**	*Scopuloides hydnoides*	GEL3859	AJ406573	–
*Scopuloides hydnoides**	*Scopuloides hydnoides*	GEL3139	AJ406574	–
*Steccherinum ochraceum**	*Steccherinum ochraceum*	KHL11902 (GB)	JQ031130	–
*Steccherinum ochraceum**	*Steccherinum ochraceum*	Ryberg sn. (GB)	EU118670	–
Specimens "incertae sedis"	*Mycoacia aurea*	GEL5339	AJ406535	–
	Mycoacia aurea	NH14434	AY586691	–
	Phlebia setulosa	PH106520, culture	GU461311	–
	Phlebia setulosa	PH11749, culture	GU461312	–
	Phlebia setulosa	PH5105, culture	GU461313	–
	Phlebia setulosa	AH31879	GQ259417	–
	Phlebia subochracea	FCUG 1161, culture	AF141630	–
	Phlebia subochracea	KGN 162/95 (GB)	EU118656[b]	EU118656[b]
	Phlebia suserialis	FCUG1434, culture	AF141631	–
	Phlebiella griseofulva	GEL4492	AJ406517	–

[a]Names as indicated in Floudas & Hibbett (2015)

[b]Unpublished sequence

[c]These sequences contain part of SSU, complete ITS region (ITS1 + 5.8S + ITS2) and D1-D2 of LSU nrDNA.

EMBL/GenBank/DDBJ databases (Cochrane et al. 2011), mainly from Hibbett et al. (2000), Parmasto and Hallenberg (2000), Thorn et al. (2000), Hibbett and Binder (2002), Langer (2002), Larsson et al. (2004), Binder et al. (2005), Han et al. (2005), Kim et al. (2005), Larsson (2007), Hallenberg et al. (2008), Porter et al. (2008), Moreno et al. (2011), Miettinen et al. (2012), and Sjökvist et al. (2012), Floudas and Hibbett (2015). In order to clearly identify the genus of the Macaronesian specimens, we selected reference sequences from some of the genera included in Meruliaceae by

Larsson (2007), and from genera included by Wu et al. (2010) in his clade V that covers *Phlebia* sensu stricto and several taxa with odontoid or hydnoid hymenophore. Moreover, sequences of type species of different genera listed in MycoBank (Crous et al. 2004, Robert et al. 2013, http://www.mycobank.org) as belonging to Meruliaceae were selected from EMBL/GenBank/DDBJ databases, mainly from references mentioned above (Table 1). Based on Binder et al. (2005) and Floudas and Hibbett (2015), two sequences of *Steccherinum* Gray (residual polypore clade) were included as outgroup. Where ambiguities in the alignment occurred, the alignment generating the fewest potentially informative characters was chosen (Baum et al. 1994). Alignment gaps were marked "–", unresolved nucleotides and unknown sequences were indicated with "N".

A maximum parsimony analysis (MP) was carried out; minimum length Fitch trees were constructed using heuristic searches with tree-bisection-reconnection (TBR) branch swapping, collapsing branches if maximum length was zero and with the MulTrees option on in PAUP*4.0b10 (Swofford 2003), with a default setting to stop the analysis at 100 trees. Gaps were treated as missing data. Nonparametric bootstrap (MP-BS) support (Felsenstein 1985) for each clade, based on 10,000 replicates using the fast-step option, was tested. The consistency index, CI (Kluge and Farris 1969), retention index, RI, and rescaled consistency index, RC (Farris 1989) were obtained. The maximum likelihood (ML) analysis was done in PAUP*Version 4.0b10, with the GTR+I+G model selected by this programme; for assessing branch support, 1000 non-parametric bootstrap replicates (ML-BS) were performed with the fast-step option. A third analysis was done by a Bayesian approach (Larget and Simon 1999, Huelsenbeck et al. 2001) using MrBayes 3.2 (Ronquist et al. 2012) and assuming the general time reversible model (Rodríguez et al. 1990), including estimation of invariant sites and a discrete gamma distribution with six categories (GTR+I+G), as selected by PAUP*Version 4.0b10. Two independent and simultaneous analyses starting from different random trees were run for two million generations with 12 parallel chains, and trees and model scores saved every 100th generation. The initial 1000 trees were discarded as burn-in before calculating the 50% majority-rule consensus tree and the posterior probability (PP) of the nodes, as described in Telleria et al. (2010). A combination of bootstrap proportions and posterior probabilities was used to assess the level of confidence for a specific node (Lutzoni et al. 2004; Wilson et al. 2012). The phylogenetic trees were viewed with FigTree v. 1.3.1 (http://tree.bio.ed.ac.uk/software/figtree/) and edited with Adobe Illustrator CS3 v. 11.0.2 (Adobe Systems).

For molecular characterization of the Macaronesian specimens, the ITS sequences were compared with homologous sequences retrieved from the EMBL/GenBank/DDBJ (Cochrane et al. 2011, 2016) and UNITE (Abarenkov et al. 2011, Kõljag et al. 2013, http://unite.ut.ee/cite.php) databases (Table 1), mainly from de Koker et al. (2003), Larsson (2007), Hilden et al. (2008), Wu et al. (2010), Sjökvist et al. (2012), and Floudas and Hibbett (2015).

Based on our previous phylogenetic trees obtained from LSU, two sequences of *Phlebia radiata* Fr. were selected as outgroup (AY219366, EF491867). Alignment gaps were marked "–", unresolved nucleotides and non-sequenced nucleotide positions within the data matrix were indicated with "N". A maximum parsimony analysis (MP)

was carried out under heuristic search, following the same criteria as mentioned above for LSU; maximum likelihood (ML) and Bayesian approaches were also performed, using the GTR+I+G as selected by PAUP*Version 4.0b10 and MrModeltest 2.3. The ML and Bayesian analyses were done with the same programs, and followed the same criteria as mentioned above for LSU.

Alignments and phylogenetic trees have been deposited at TreeBase: http.//purl.org/phylo/tree-base/phylows/study/TB2:S21012

Results

Sixteen new sequences from the Macaronesian specimens were generated in this study (Table 1). The LSU sequence contains the domain D1-D2, and the ITS sequence the regions ITS1, 5.8S nrDNA and ITS2.

LSU analyses

The LSU dataset contains 57 sequences and 908 aligned positions, of which 682 were constant, 82 parsimony uninformative, and 144 parsimony-informative. Maximum parsimony analysis yielded 100 most parsimonious trees (613 steps long, CI = 0.4731, HI = 0.6164, RI = 0.7399) under a heuristic search. Almost identical tree topologies were generated after parsimony and Bayesian analyses. The 50% majority-rule consensus tree from the Bayesian analysis is shown in Fig. 1, with percentage of bootstrap (MP-BS and ML-BS) and posterior probabilities indicated on the branches. The circumscription of clade V from Wu et al. (2010) is indicated in this figure.

All sequences obtained from Macaronesian specimens cluster in a supported clade (MP-BS = 70%, ML-BS = 80 %, PP = 1.0), with sequences from de Koker et al. (2003) and Floudas and Hibbett (2015) under *Hydnophlebia*. Most sequences are distributed over two supported clades, one containing four specimens from São Vicente (MP-BS = 96%, ML-BS = 95 %, PP = 1.0), and the other three specimens from Canary Islands (MP-BS = 93%, ML-BS = 95 %, PP = 0.98). Specimen 19071Tell., from Fogo Island, appears together with sequences KP135334 and KP135218, under *H. omnivora* 1 and *H. omnivora* 2 in Floudas and Hibbett (2015); although this relationship is not well supported (MP-BS = 93%, ML-BS = 95 %, PP = 0.98). The two *H. chrysorhizon* sequences (AF139967 and KP135217 from previous authors) form a fairly well supported clade with the specimens from Saõ Vicente (MP-BS = 61%, ML-BS = 65 %, PP = 1.0).

ITS analyses

The ITS nrDNA dataset contains 26 sequences and 851 aligned positions, of which 575 were constant, 103 parsimony uninformative, and 173 parsimony-informative. After heuristic search, the 100 trees had 447 steps, CI = 0.7136, HI = 0.3798 and RI

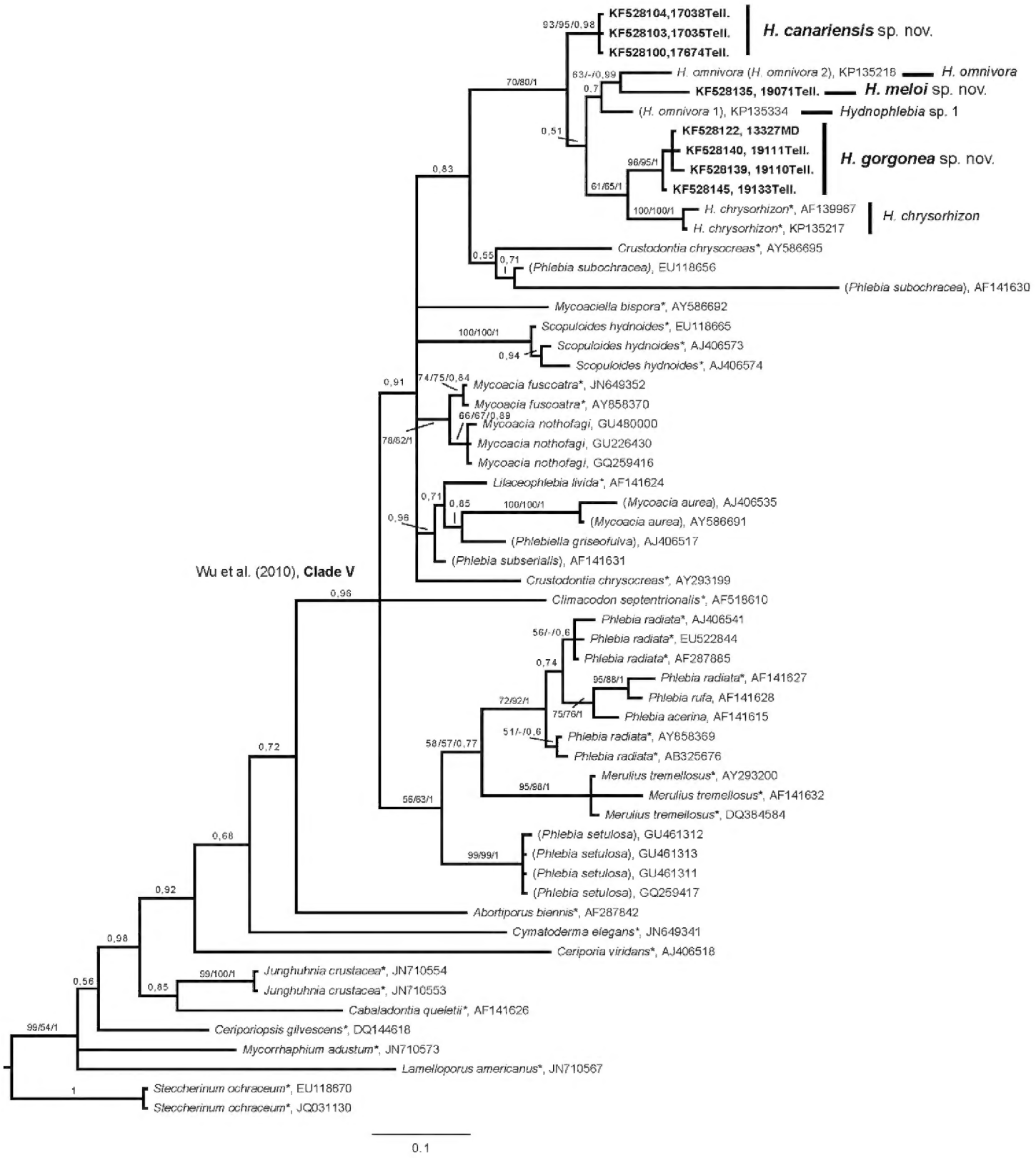

Figure 1. The 50% majority rule Bayesian tree inferred from D1-D2 LSU nrDNA assuming the GTR + I + G model of corticioid fungi included in Table 1. Parsimony bootstrap values (> 50%) maximum likelihood bootstrap values (> 50%) and Bayesian posterior probabilities (> 0.95) are indicated on the branches. Clade V from Wu et al. (2010) is indicated. Taxon name between parentheses indicate specimens with uncertain generic placement. Sequences of the new species described in this paper, *H. canariensis, H. gorgonea* and *H. meloi* are in bold. The asterisk (*) after the taxon names denotes type species of the genus.

= 0.7831. Almost identical tree topologies were generated after parsimony (data not shown), maximum likelihood (data not shown) and Bayesian analyses. The 50% majority-rule consensus tree from the Bayesian analysis is shown in Fig. 2, with percentage of bootstrap (MP-BS and ML-BS), and posterior probabilities indicated on the branches.

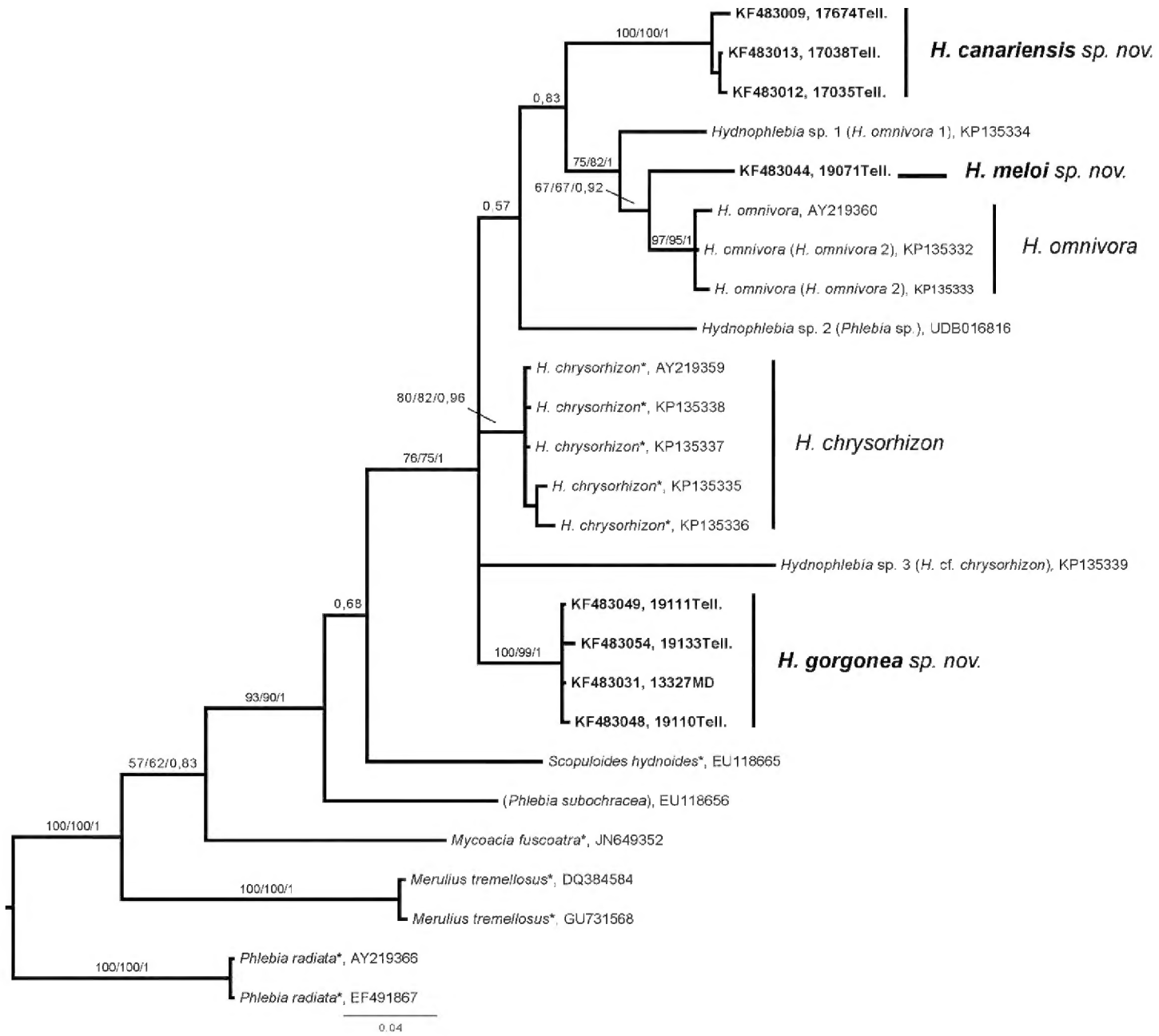

Figure 2. The 50% majority rule Bayesian tree inferred from ITS nrDNA assuming the GTR + I + G model of corticioid fungi included in Table 1. Parsimony bootstrap values (> 50%), maximum likelihood bootstrap values (> 50%) and Bayesian posterior probabilities (> 0.95) are indicated on the branches. Taxon name between parentheses indicate specimens with uncertain generic placement. Sequences of the new species described in this paper, *H. canariensis, H. gorgonea* and *H. meloi* are in bold. The asterisk (*) after the taxon names denotes type species of the genus.

Similar to the LSU analyses, the sequences from Macaronesian specimens form a clade (MP-BS = 76%, ML-BS = 75%, PP = 1.0), together with downloaded sequences of *Hydnophlebia* from the USA (Arizona, Florida, Illinois, New York and Puerto Rico) and Canada, identified in Floudas and Hibbett (2015) as *H. chrysorhizon*, *H.* cf. *chrysorhizon*, *H. omnivora* 1 and *H. omnivora* 2; as well as sequences of *H. chrysorhizon* from Illinois and *H. omnivora* from Arizona published by de Koker et al. (2003) that we consider represent the modern interpretation of these two species. Sequence UDB016816 from Madagascar, in Fig. 2, labelled as *Hydnophlebia* sp. 2, (under *Phlebia* sp. in UNITE database) also clusters in this clade.

The five sequences from Canada and the USA identified as *H. chrysorhizon* grouped in a highly supported clade (MP-BS > 80%, ML-BS > 82%, PP = 1.0). The sequences

UDB016816, labelled *Hydnophlebia* sp. 2 from Madagascar, and KP135339, labelled *Hydnophlebia* sp. 3 (*H.* cf. *chrysorhizon* in Floudas and Hibbett 2015) from Puerto Rico, did not group with other *Hydnophlebia* sequences.

The new sequences generated for this work are distributed over three clades. These clades are here described in the order they occur from top to bottom in Fig. 2.

The first group (MP-BS = 100%, ML-BS = 100%, PP = 1.0) contains sequences of 17035Tell., 17038Tell., and 17674Tell. from El Hierro and Fuerteventura Islands, collected on different substrates.

A second clade (MP-BS > 75%, ML-BS > 82%, PP = 1.0) encloses specimen 19071Tell., from Fogo Island, collected on *Sarcostemma daltonii* Decne (Asclepiadaceae), and the sequence indicated in Fig. 2 as *Hydnophlebia* sp. 1 (*H. omnivora* 1 in Floudas and Hibbett 2015) and three sequences of *Hydnophlebia omnivora* (two of them as *H. omnivora* 2 in Floudas and Hibbett 2015).

Sequences of 13327MD, 19110Tell., 19111Tell., and 19133Tell., all from São Vicente Island on *Prosopis juliflora* (Sw.) DC. (Fabaceae), are distributed in a third clade (MP-BS = 100%, ML-BS = 99%, PP = 1.0).

Taxonomy

Hydnophlebia Parmasto, Izv. Akad. Nauk Estonsk. SSR, Ser. Biol. 16: 384. 1967

Type species. *Hydnum chrysorhizon* Torr. in Eaton, Manual Bot.: 309. 1822

Basidioma resupinate, separable, generally reddish orange yellow. Hymenophore hydnoid, with aculei up to 0.5–1.5 mm long, conical to cylindrical. Margin with strands. Hyphal system monomitic with scattered clamps, subicular and strand hyphae thick-walled, colorless to yellowish, encrusted, aculei and subhymenial hyphae thin-walled, also colorless. Cystidia cylindrical to ventricose, colorless, thin-walled, sometimes few. Basidia cylindrical to subclavate, with 4 sterigmata, basal clamp absent. Spores cylindrical, ellipsoid to subglobose, smooth, thin-walled.

Key to species of *Hydnophlebia*

1 Spores narrowly ellipsoid to cylindrical, 4–6 × 2–3 µm (L/W = 1.9). Basidiome orange brown in dry specimens, reddish orange to deep orange in fresh material. Strands very long, yellowish to cream in dry material and reddish orange in fresh specimens, up to 1 mm diam ..... **2. *H. chrysorhizon***

– Spores ellipsoid, broadly ellipsoid or subglobose (L/W ≤ 1.6) **2**

2 Spores subglobose, 4–5.5 × 3–4 µm (L/W = 1.2). Basidiome yellowish white to pale orange-yellow in dry specimens. Margin fimbriate, yellowish white, with strands poorly developed. Cystidia cylindrical, 40–55 × 3–4 µm..... ..... **4. *H. meloi***

– Spores ellipsoid to broadly ellipsoid (L/W ≥ 1.3) **3**

3 Basidiome in small and poorly developed patches, cream-coloured in dry specimens. Clamps present in strand hyphae. Cystidia cylindrical slightly tapered at the apex, 40–70 × 4–5 µm. Spores ellipsoid, 5–6.5 × 3–4 µm (L/W = 1.6) ..... **5. *H. omnivora***

– Basidiome broadly effuse, orange-yellow to brilliant orange-yellow. Clamps absent in strand hyphae **4**

4 Basidiome light orange-yellow in dry specimens. Margin fimbriate, with white, well developed strands. Cystidia of two types, cylindrical with slightly tapered apex and ventricose with subulate apex, 45–55 × 3–5 µm. Spores ellipsoid, 5–7 × 3–4.5 µm (L/W = 1.5) ..... **1. *H. canariensis***

– Basidiome light to brilliant orange-yellow in dry specimens. Margin fimbriate with poorly developed strands. Cystidia cylindrical, sometimes capitate, to ventricose, 45–55 × 4–6 µm. Spores ellipsoid to broadly ellipsoid, 5–7 × 4–4.5 µm (L/W = 1.4) ..... **3. *H. gorgonea***

1. *Hydnophlebia canariensis* Telleria, M. Dueñas & M.P. Martín, sp. nov.
MycoBank MB815729
Figs 3, 4

Diagnosis. This species can be recognized by the orange-yellow basidiome, hydnoid hymenophore with long aculei, up to 1,5 mm, white subiculum, and well-developed white strands. Spores ellipsoid 5–7 × 3–4.5 µm (L/W = 1.5).

Type. Spain. Canary Islands: El Hierro, Frontera, Sabinar de la Dehesa, 27°44'43"N; 18°07'02"W, 610 m alt., on unidentified wood, 26 January 2007, M.T. Telleria, 17035Tell. (holotype: MA-Fungi 86622). LSU sequence KF528103, ITS sequence KF483012.

Etymology. Named after the Canary Islands where the holotype and paratypes were collected.

Description. Basidiome resupinate, effuse, membraneous to ceraceous, yellow (82. v. Y) in fresh specimens and light orange-yellow (70. l. OY) in dry. Hymenophore hydnoid, aculei conical, 0.5–1.5 mm long. Subiculum byssoid, white. Margin fimbriate, white, with well-developed white strands.

Hyphal system monomitic; subicular hyphae 6–8 µm wide, with clamps, thin to thick-walled; strand hyphae 7–11 µm wide, without clamps, thick-walled; aculei hyphae 4–5 µm wide, without clamps, thin-walled and growing perpendicular to the substrate; subhymenial hyphae 3–4 µm wide, without clamps, thin-walled, and loosely interwoven. Cystidia of two types: cylindrical with slightly tapered apex and ventricose with subulate apex, thin-walled, 45–55 × 3–5 µm. Basidia cylindrical to subclavate, 24–28 × 4–6 µm, with 4 sterigmata, basal clamp absent. Spores ellipsoid 5–7 × 3–4.5 µm (L/W = 1.5), thin-walled, colorless, smooth.

Ecology and distribution. On decayed wood and plant debris in arid and semi-arid habitats; known only from the Canary Islands.

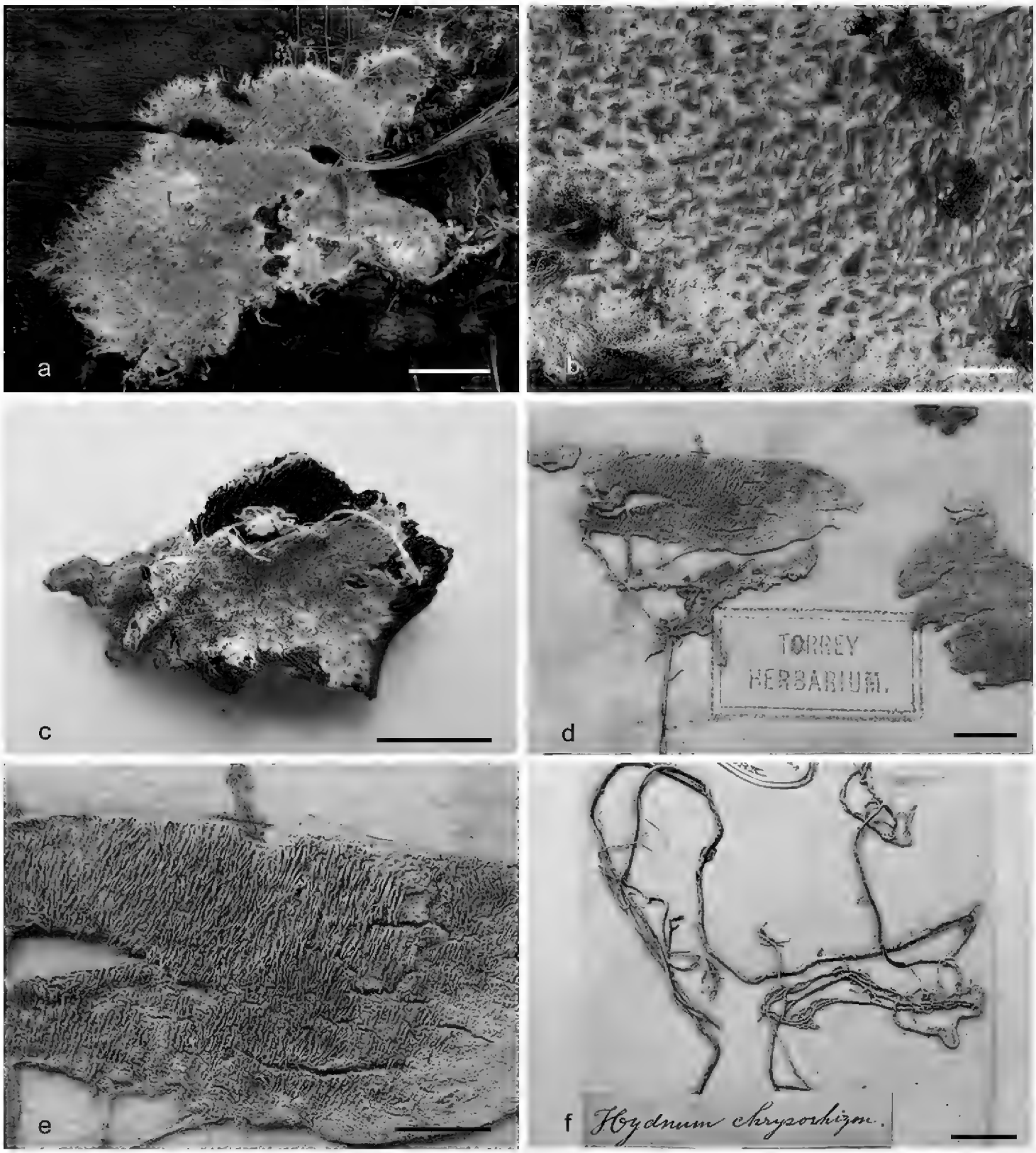

Figure 3. *Hydnophlebia canariensis.* **a**, **b** Collection 17035Tell., MA-Fungi 86622, holotype, basidiome, wet (a) and hymenophore, dry specimen (b) **c** Collection 17038Tell. MA-Fungi 86623, basidiome, dry specimen. *Hydnophlebia chrysorhizon*. Collection NY, lectotype **d** Basidiome, dry specimen **e** Hymenophore, dry specimen **f** Strands, dry specimen. Scale bars: **a, e** = 5 mm; **b** = 1.5 mm; **c, d, f** = 1 cm.

Other specimens examined. Spain. Canary Islands: El Hierro, Frontera, Sabinar de la Dehesa, 27°44'43"N; 18°07'02"W, 610 m alt., on unidentified wood, 26 January 2007, M.T. Telleria, 17038Tell. (MA-Fungi 86623), LSU sequence KF528104, ITS sequence KF483013. Fuerteventura, Pájara, Parque Natural de Jandía, Valle de los Mosquitos, 28°04'36"N; 14°25'23"W, 99 m alt., on *Launaea arborescens*, 05 December 2007, M.T. Telleria, 17674Tell. (MA-Fungi 86619), LSU sequence KF528100, ITS sequence KF483009.

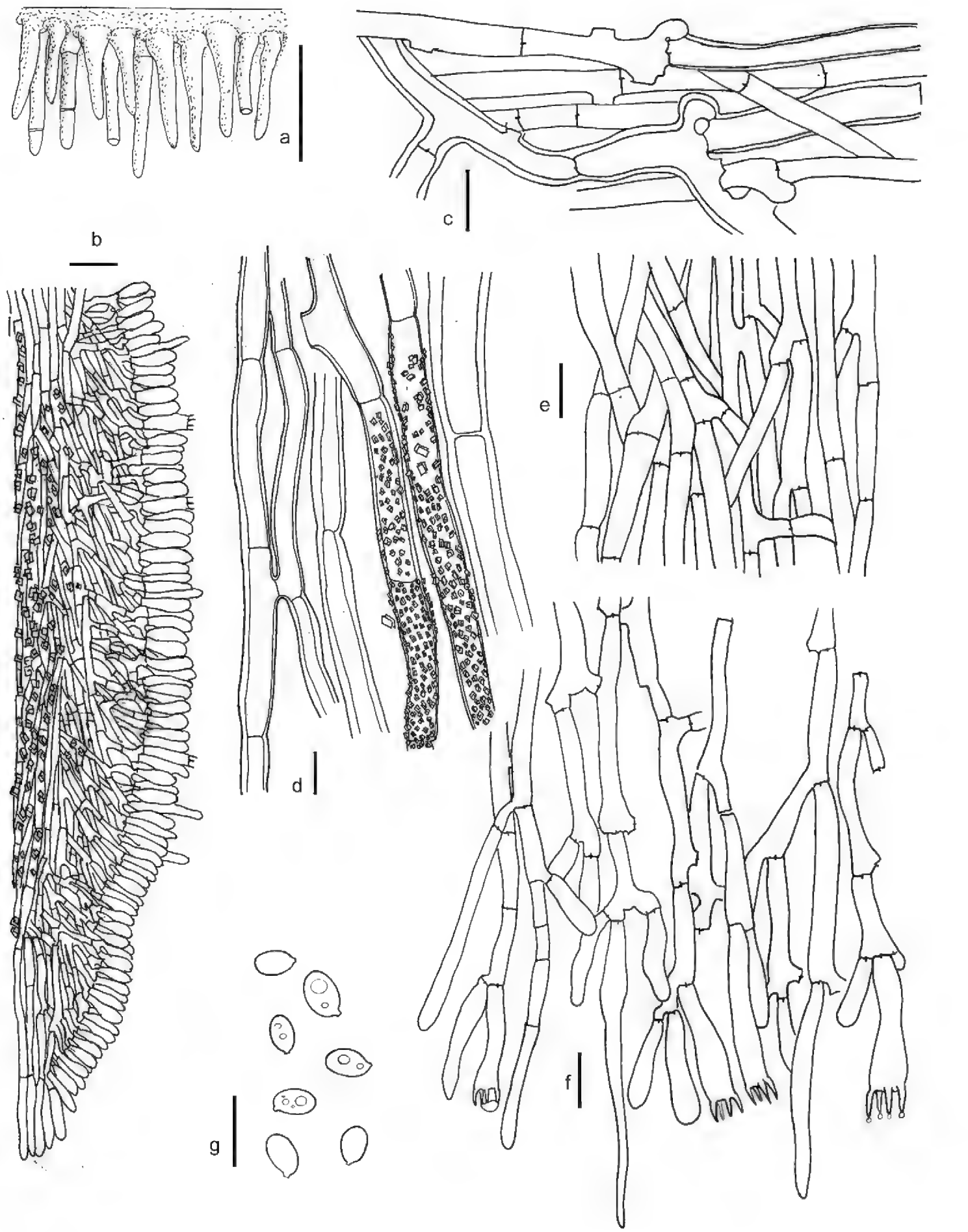

Figure 4. *Hydnophlebia canariensis*. Collection 17035Tell., MA-Fungi 86622, holotype **a** Hymenophore **b** Vertical section through an aculei **c** Subicular hyphae **d** Strand hyphae **e** Aculei hyphae **f** Subhymenial hyphae, cystidia, and basidia **g** Spores. Scale bars: **a** = 1 mm; **b** = 25 µm; **c–g** = 10 µm. Drawing by M. Dueñas.

2. *Hydnophlebia chrysorhizon* (Torr.) Parmasto, Izv. Akad. Nauk Estonsk. SSR, Ser. Biol. 16: 384. 1967

Figs 3, 5

Basionym. *Hydnum chrysorhizon* Torr. in Eaton, Manual Bot.: 309. 1822

Type. USA, *Hydnum chrysorhizon* Torr. in Eaton Man. 3ed. p. 309. 237, C. C., Steward. In herbarium NY! (lectotype, designated by Burdsall 1985).

Description. Basidiome resupinate, effuse, membraneous, easily separable, orange-brown in dry specimens, reddish orange to deep orange in fresh material (Burdsall and Nakasone 1978, Lindsey and Gilbertson 1975, Burdsall 1985, Maekawa 1993). Hymenophore hydnoid, aculei dense, conical to subcylindrical, 1–1.6 mm long. Margin with strands very long and well developed, yellowish to cream in dry specimens, reddish orange in fresh specimens (Burdsall 1985), up to 1 mm diam.

Hyphal system monomitic; subicular hyphae 7–10 µm wide, with clamps, thick-walled, colorless to pale yellow, densely encrusted with colorless crystals and loosely interwoven; strand hyphae 10–17 µm wide, without clamps, thick-walled, colorless, also encrusted; aculei hyphae 4–6 µm wide, with scattered clamps, thin-walled, colorless, and oriented perpendicular to the substrate; subhymenial hyphae 5–7 µm wide, without clamps, thin-walled, colorless, densely interwoven, short-celled. Cystidia not seen, but according to Burdsall (1985) few, cylindrical, thin-walled, hyaline, short, 18–40 × 4.5–6 µm. Basidia clavate, 15–21 × 4–6 µm, with 4 sterigmata, basal clamp absent. Spores narrowly ellipsoid to cylindrical, 4–6 × 2–3 µm (L/W = 1.9), thin-walled, colorless, smooth.

Ecology and distribution. On decayed wood. Described from New York (Eaton 1822), this species has been reported from: Africa: Cameroon, (Roberts 2000), and Seychelles (Hjortstam and Ryvarden 2009); North America: USA, Arizona, Florida, Maryland, Mississippi, New York, North Carolina, South Carolina, Tennesse, Wisconsin (Lindsey and Gilbertson 1975, Burdsall and Nakasone 1978, Burdsall 1985, Nakasone 2012); South America: Argentina, Venezuela, Brazil (Hjortstam and Ryvarden 2007); Meso America: Puerto Rico (Hjortstam and Ryvarden 2009), as well as Saint Vincent and the Grenadines (Nakasone 2012); Asia: Japan (Maekawa 1993).

Other specimens examined. USA. Ohio, Hamilton Co. Sharon Woods County Park, on *Quercus* sticks, 13 October 1973, W.B. & V.G. Cooke 48958. New York, New Dorp, Staten Island, 17 October 1896, col. L.M. Underwood.

Remarks. This species has very long and well-developed strands and, microscopically, it is the only species in the genus with spores narrowly ellipsoid to cylindrical (L/W = 1.9) and scattered clamps in the aculei hyphae.

Based on morphological analyses, Burdsall (1985) considered *Hydnum fragilissimum* Berk. & M.A. Curtis, *Hydnum ischnodes* Berk., and *Hydnum chrysocomum* Underw. as synonyms of *H. chrysorhizon*; and according to Nakasone (2012) *Hydnum schweinitzii* Berk. & M.A. Curtis, *Hydnum chrysodon* Berk. & M.A. Curtis, and *Merulius elliottii* Massee are other synonyms.

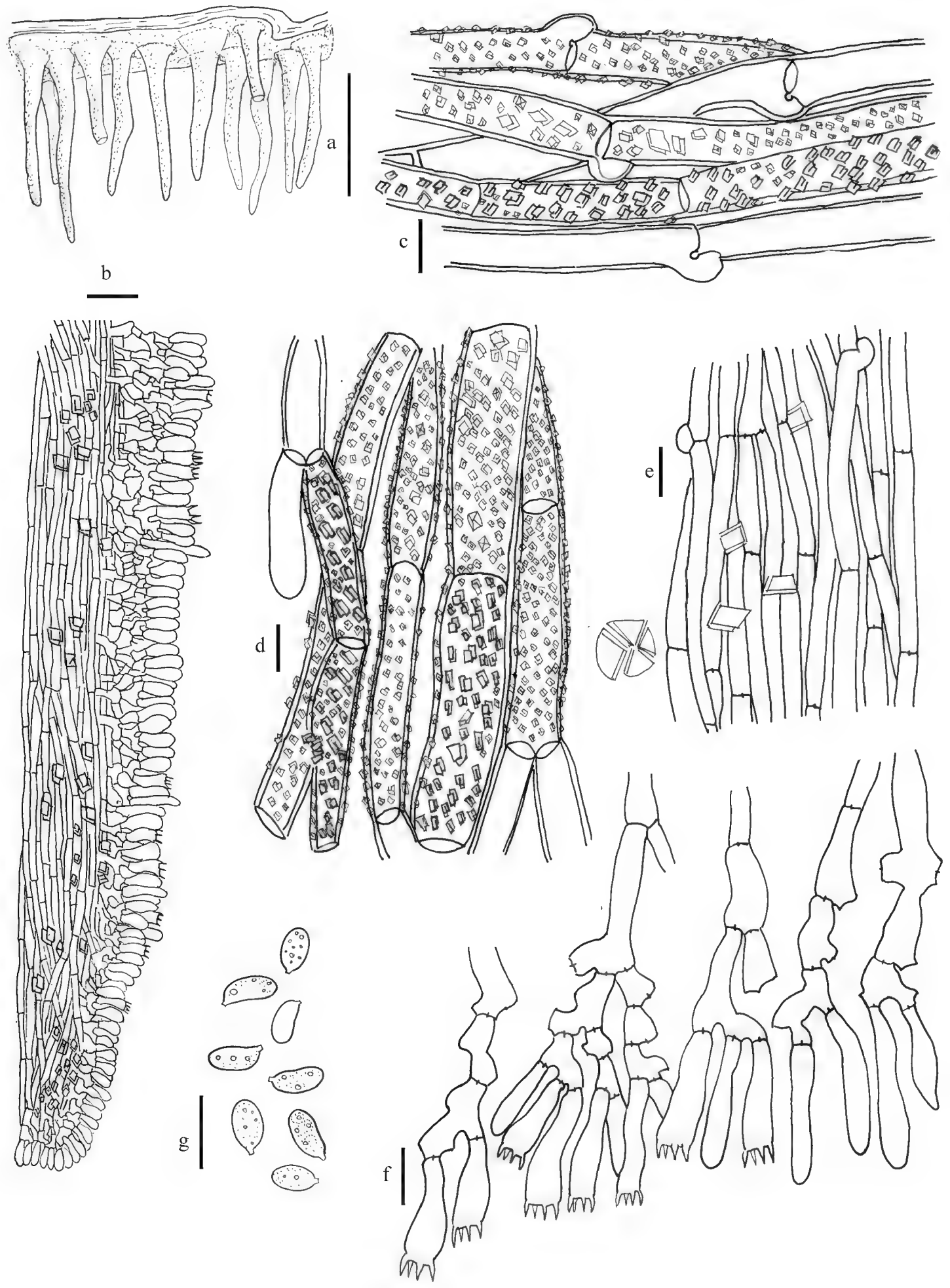

Figure 5. *Hydnophlebia chrysorhizon*. Collection NY, lectotype **a** Hymenophore **b** Vertical section through an aculei **c** Subicular hyphae **d** Strand hyphae **e** Aculei hyphae **f** Subhymenial hyphae and basidia **g** Spores. Scale bars: **a** = 1mm; **b** = 25 µm; **c–g** = 10 µm. Drawing by M. Dueñas.

3. *Hydnophlebia gorgonea* Telleria, M. Dueñas & M.P. Martín, sp. nov.

MycoBank MB815730

Figs 6, 7

Diagnosis. Morphologicaly this species is similar to *Hydnophlebia canariensis*, but can be distinguished by the strands, well developed in *H. canariensis* and poorly so in *H. gorgonea*. Spores ellipsoid to broadly ellipsoid 5–7 × 4–4.5 µm (L/W = 1.4).

Type. Cape Verde. São Vicente: Mindelo, Ribeira da Vinha, 16°51'49"N; 25°00'09"W, 10 m alt., on *Phoenix atlantica*, 26 September 2010, M.T. Telleria, 19111Tell. (holotype: MA-Fungi 86659), LSU sequence KF528140, ITS sequence KF483049.

Etymology. Named after Gorgades, an ancient name for the Cape Verde Islands, Atlantic Ocean.

Description. Basidiome resupinate, effuse, membraneous, easily separable, light orange-yellow (70. l. OY) to brilliant orange-yellow (67. brill. OY). Hymenophore hydnoid, aculei conical, 0.6–1 mm long. Margin fimbriate, white, with poorly developed strands.

Hyphal system monomitic; subicular hyphae 6–8 µm wide, with clamps, thin- to thick-walled, loosely interwoven, hyaline, encrusted with colorless crystals; strand hyphae 12–15 µm wide, without clamps, thick-walled, sometimes gelatinous and also encrusted; aculei hyphae 3.5–4.5 µm wide, without clamps, thin-walled, colorless, growing perpendicular to the substrate; subhymenial hyphae 4.5–8 µm wide, without clamps, thin-walled, colorless, loosely interwoven, and short- to long-celled. Cystidia cylindrical to ventricose, sometimes capitate, thin-walled, 45–55 × 4–6 µm. Basidia cylindrical to subclavate, 22–24 × 6–8 µm, with 4 sterigmata, basal clamp absent. Spores ellipsoid to broadly ellipsoid 5–7 × 4–4.5 µm (L/W = 1.4), thin-walled, colorless, smooth.

Ecology and distribution. This species is known from only two localities of São Vicente Island, Cape Verde Archipelago, on decayed wood of *Phoenix atlantica* and *Prosopis juliflora* in arid habitats.

Other specimens examined. Cape Verde. São Vicente: Mindelo, Ribeira da Vinha, 16°51'49"N 25°00'09"W, 10 m alt., on *Prosopis juliflora,* 26 September 2010, M.T. Telleria, 19110Tell. (MA-Fungi 86658), LSU sequence KF528139, ITS sequence KF483048; M. Dueñas, 13327MD (MA-Fungi 86642), LSU sequence KF528122, ITS sequence KF483031. São Vicente: Ermida, 16°50'26"N; 24°57'23"W, 100 m alt., on *Prosopis juliflora*, 26 September 2010, M.T. Telleria, 19133Tell. (MA-Fungi 86664), LSU sequence KF528145, ITS sequence KF483054.

4. *Hydnophlebia meloi* Telleria, M. Dueñas & M.P. Martín, sp. nov.

MycoBank MB815731

Figs 6, 8

Diagnosis. Similar to *Hydnophlebia omnivora* but differs in having subglobose spores, 4–5.5 × 3–4 µm (L/W = 1.2), instead of ellipsoid, 5–6.5 × 3–4 µm (L/W = 1.6). This is the only species in the genus with subglobose spores.

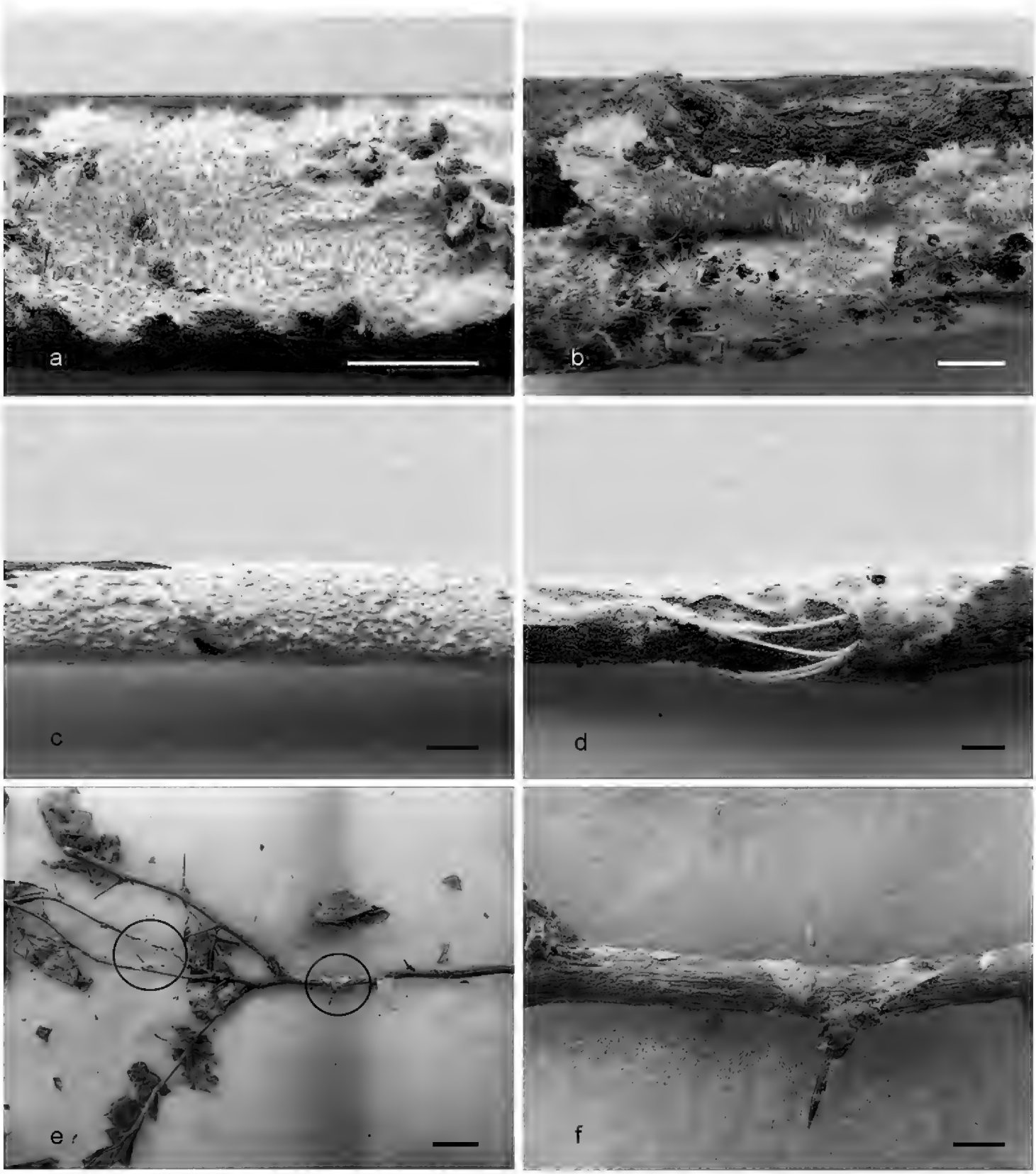

Figure 6. *Hydnophlebia gorgonea.* **a** Collection 19111Tell., MA-Fungi 86659, holotype, basidiome, dry specimen **b** Collection 19133Tell., MA-Fungi 86664, basidiome, dry specimen. *Hydnophlebia meloi* **c**, **d** Collection 19071Tell., MA-Fungi 86654, holotype, basidiome, dry specimen (c), and margin and strands, dry specimen (d). *Hydnophlebia omnivora* **e** Collection 5267 C.R. Shear coll., BPI, holotype **f** Basidiome, dry specimen. Scale bars: **a–b** = 5 mm; **c–d, f** = 2 mm; **e** = 10 mm.

Type. Cape Verde. Fogo: Mosteiros, Miradouro, 15°01'41"N; 24°19'13"W, 283 m alt., on *Sarcostemma daltonii*, 24 September 2010, M.T. Telleria, 19071Tell. (holotype: MA-Fungi 86654), LSU sequence KF528135, ITS sequence KF483044.

Etymology. Named after Ireneia Melo, colleague and friend, Portuguese mycologist from the Botanical Garden of the University of Lisbon.

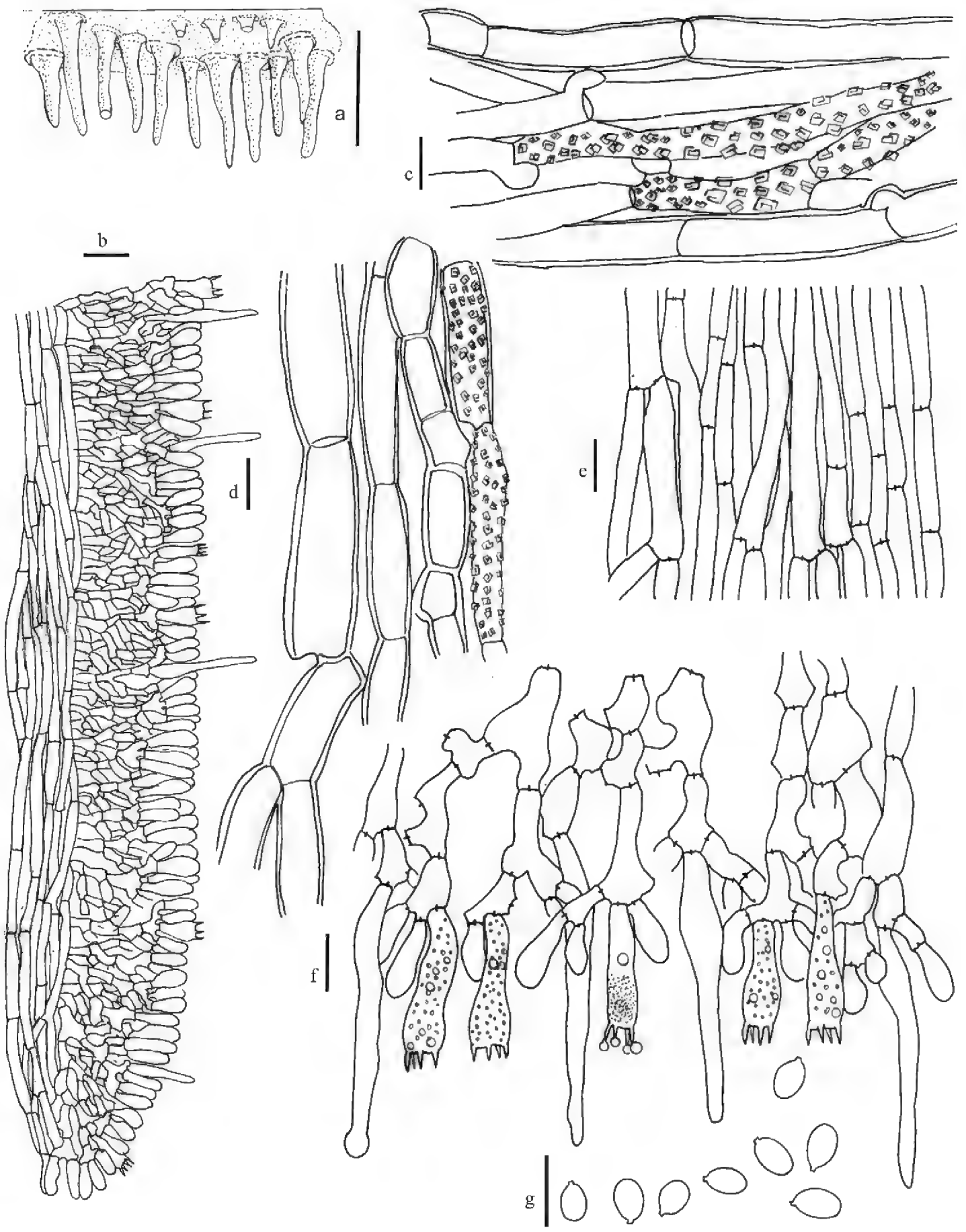

Figure 7. *Hydnophlebia gorgonea.* Collection 19111Tell., MA-Fungi 86659, holotype **a** Hymenophore **b** Vertical section through an aculei **c** Subicular hyphae **d** Strand hyphae **e** Aculei hyphae **f** Subhymenial hyphae, cystidia, and basidia **g** Spores. Scale bars: **a** = 1 mm; **b** = 25 µm; **c–g** = 10 µm. Drawing by M. Dueñas.

Description. Basidiome resupinate, effuse, membraneous to ceraceous, yellowish white (92. y White) to pale orange-yellow (73. p. OY) in dry specimens. Hymenophore hydnoid, aculei conical, 0.5–1 mm long, in dried specimens usually broken. Margin fimbriate, yellowish white, with strands.

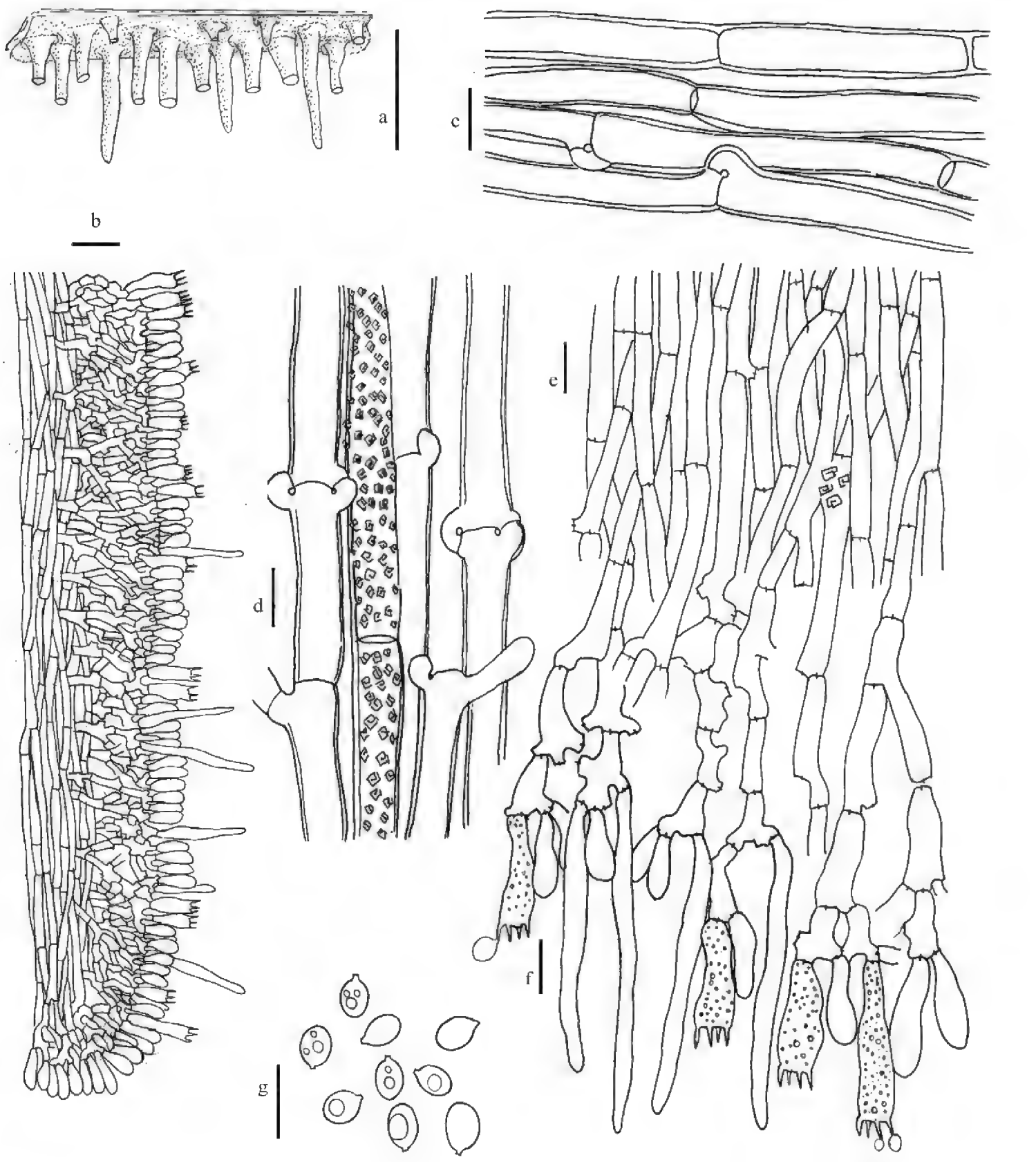

Figure 8. *Hydnophlebia meloi.* Collection 19071Tell., MA-Fungi 86654, holotype **a** Hymenophore **b** Vertical section through an aculei **c** Subicular hyphae **d** Strand hyphae **e** Aculei hyphae **f** Subhymenial hyphae, cystidia, and basidia **g** spores. Scale bars: **a** = 1 mm; **b** = 25 µm; **c–g** = 10 µm. Drawing by M. Dueñas.

Hyphal system monomitic; subicular hyphae 6–7.5 µm wide, with clamps, thick-walled, loosely interwoven; strand hyphae 6–7.5 µm wide, with clamps occasionally double, thick-walled, sometimes encrusted with colorless crystals; aculei hyphae 3.5–4.5 µm wide, without clamps, thin-walled, growing perpendicular to the substrate; sub-

hymenial hyphae 3.5–4.5 µm wide, without clamps, thin-walled, loosely interwoven, short- to long-celled. Cystidia cylindrical, thin-walled, 40–55 × 3–4 µm. Basidia cylindrical to subclavate, 18–26 × 5–7 µm, with 4 sterigmata, basal clamp absent. Spores subglobose 4–5.5 × 3–4 µm (L/W = 1.2), thin-walled, colorless, smooth.

Distribution. Rocky steep slopes, on *Sarcostemma daltonii*, endemic climbing herb of Cape Verde Archipelago. Only known from the type locality in Fogo Island.

Other specimens examined. Cape Verde. Fogo: Mosteiros, Miradouro, 15°01'41"N; 24°19'13"W, 283 m alt., on *Sarcostemma daltonii*, 24 September 2010, M.T. Telleria, 19072Tell. (MA-Fungi 90746).

5. *Hydnophlebia omnivora* (Shear) Hjortstam & Ryvarden, Synopsis Fungorum 26: 10-23. 2009

Figs 6, 9

Basionym. *Hydnum omnivorum* Shear, J. Agric. Res. 30: 476. 1925

Type. USA, C.L.S. Type on Osage Orange [*Macura pomifera*], near Paris, Texas. C.R. Shear coll. Sept. 1903, no. 5267. In herbarium BPI! (holotype).

Description. Basidiome effuse in small and poorly developed patches, cream-coloured in dry specimens. Hymenophore, according to Burdsall (1985), hydnoid, aculei conical to subcylindrical, 0.6–1 mm long; broken or poorly developed in type material. Margin floccose to fibrillose, white, with strands poorly developed.

Hyphal system monomitic; subicular hyphae 8–11 µm wide, with clamps occasionally double, thick-walled, loosely interwoven; strand hyphae 5–9 µm wide, with a few clamps, thick-walled, colorless; aculei hyphae 4–5 µm wide, without clamps, thin-walled, growing perpendicular to the substrate; subhymenial hyphae 5–6 µm wide, without clamps, thin-walled, densely interwoven, short-celled. Cystidia cylindrical, slightly tapered to apex, thin-walled, 40–70 × 4–5 µm. Basidia cylindrical to subclavate, 17–21× 6–7 µm, with 4 sterigmata, basal clamp absent. Spores ellipsoid, 5–6.5 × 3–4 µm (L/W = 1.6), thin-walled, colorless, smooth.

Ecology and distribution. Described from Texas (Shear 1925). According to Burdsall (1985) this species is distributed in the arid regions of southwestern United States, and probably into southern California and northern Mexico. Also reported from Florida (Ginns and Lefebvre 1993) and Uruguay (Martínez and Nakasone 2005).

Remarks. Molecular analyses indicate that this species is related to *H. meloi*. Morphologically they can be distinguised by the shape and size of spores, subglobose 4–5.5 × 3–4 µm in *H. meloi*, and ellipsoid 5–6.5 × 3–4 µm in *H. omnivora*.

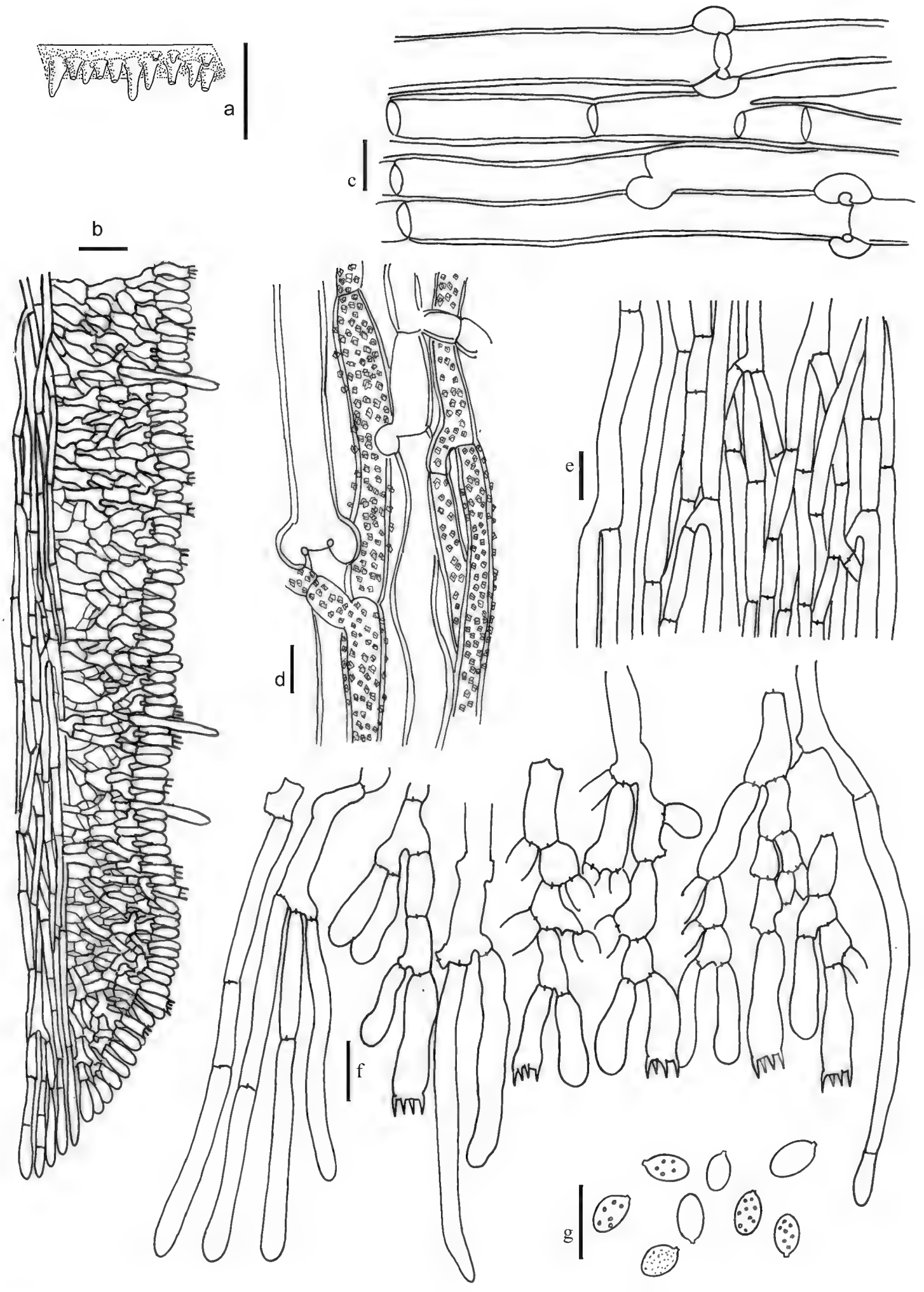

Figure 9. *Hydnophlebia omnivora*. Collection 5267 C.R. Shear coll., BPI, holotype **a** Hymenophore **b** Vertical section through an aculei **c** Subicular hyphae **d** Strand hyphae **e** Aculei hyphae **f** Subhymenial hyphae, cystidia, and basidia **g** Spores. Scale bars: **a** = 1 mm; **b** = 25 µm; **c–g** = 10 µm. Drawing by M. Dueñas.

Discussion

In this study a taxonomic analysis of *Hydnophlebia*, based on morphological and molecular data, is provided. *Hydnophlebia* has been confused with *Phanerochaete* and the two species included, *Hydnophlebia chrysorhizon* and *Hydnophlebia omnivora*, were assigned to the latter genus (Burdsall 1985).

For a long time, *Hydnophlebia* was considered a monospecific genus; however, based on the molecular analyses, both LSU and ITS sequences, as well as a point-by-point comparison of the morphological characters, five species can be discriminated, two already described by other authors (*H. chrysorhizon* and *H. omnivora*), and the three new species from Macaronesia described here (*H. canariensis, H. gorgonea*, and *H. meloi*).

Moreover our results show that three other species could be described, although more collections should be analysed: 1) *Hydnophlebia* sp. 1 under *H. omnivora* 1 in Floudas and Hibbett (2015); 2) *Hydnophlebia* sp. 2 under *Phlebia* sp. from Madagascar in UNITE database; and 3) *Hydnophlebia* sp. 3 under *Hydnophlebia* cf. *chrysorhizon* in Floudas and Hibbett (2015).

Acknowledgements

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